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Arboreta reveal the invasive potential of several conifer species in the temperate forests of western Europe

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Abstract

Identifying emerging invasive species is a priority to implement early preventive and control actions. In terms of the number of invasive tree species, forestry represents the second largest pathway of introduction, with an invasive debt likely existing for alien conifers in Europe. In the early 1900s, a network of arboreta was established in southern Belgium to assess the wood production potential of prospective conifer and broadleaved species. Here, we use eight arboreta as natural experiments to identify alien conifers presenting invasive behavior. Through systematic sampling, we quantified the natural regeneration of alien conifers and recorded local environmental variables. For each species, regeneration density, dispersal distances, and age structure were analyzed. Generalized mixed effects models were fitted to test the effect of planted area and tree-stand type on regeneration. The environmental space occupied by regenerating alien conifers was evaluated using principal component analysis. Out of 31 planted alien species, 15 (48%) were identified in natural regeneration, of which eight (26%) exhibited important regeneration density and dispersal distances. The most invasive species were *Tsuga heterophylla* and *Abies grandis*, confirming earlier field observations. Both large planted areas and areas planted with alien conifer species increased the density of regeneration. Species that had the highest regeneration density tolerated a wide range of environmental conditions, including shaded understory, which could lead to the invasion of mature, undisturbed forests. This study showed that 17% of the studied alien conifers are potentially invasive because they show important regeneration, long-distance dispersal, and, of importance, have already produced offspring that have matured and are capable of creating new satellite populations. In conclusion, our results provide a guideline for future planting operations, recommending extreme caution when planting these species in the temperate forests of Western Europe.

Keywords

Arboretum, dispersal, gymnosperm, invasiveness, non native trees, propagule pressure, regeneration

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Introduction

Early identification of emerging invasive species remains one of the most challenging issues in invasion science. Following numerous introductions worldwide for ornamental or production purposes, many tree species have since been recognized as invasive (Dodet and Collet 2012; Richardson et al. 2014). Rejmánek (2014) identified 76 tree species exhibiting invasive behavior in Europe. Alien woody species have the capacity to modify the structure of invaded ecosystems substantially and cause extensive ecological and economical damage (Lamarque et al. 2011; Pyšek 2016). In addition, management actions are often taken too late, when the species are already widespread and when the management costs of mitigation are prohibitive (Rejmánek and Pitcairn 2002; van Wilgen and Richardson 2014).

Most problematic tree species in Europe were introduced decades or centuries ago (Nyssen et al. 2016) and actively spread by human. In parallel, some dispersed outside their cultivation areas and spread *via* small satellite populations over kilometers (Mack 2005; Pyšek and Richardson 2012). Delays between the installation of these satellite populations and their capacity to reproduce create an important lag phase between the introduction of a species in a new area and its invasion of natural habitats (Wangen and Webster 2006). In Germany, this lag phase has been estimated to last 170 years on average for trees (Kowarik 1995). Future invasive species might, therefore, already have been introduced but might not have completed the naturalization–invasion continuum, yet. This time-delayed invasion is referred to as the invasion debt (Rouget et al. 2016). Because introduction events increased during the second half of the 20th century, an invasion debt, without doubt, exists in Europe for trees (Essl et al. 2011) and must be evaluated to anticipate new invasions (Richardson and Rejmánek 2011).

When the number of introduction events increases, so does the probability of naturalization (Heger 2016). Along with the propagule pressure, several functional traits can help predict the invasiveness of plant species such as an important SLA, growth rate, height, germination rate and fitness (van Kleunen et al. 2010; Lamarque et al. 2011; Kutlvašr et al. 2019). For conifers specifically, Richardson and Rejmánek (2004) identified a small seed mass, short juvenile period and short intervals between large crops as traits associated with invasiveness.

The forestry sector has been introducing alien tree species for centuries in Europe for timber production, including many conifers from Asia and north America (Krumm and Vítková 2016; Gil-Moreno 2018). Species selected for forest plantations often originate from regions with a similar climate and present high growth rates, two factors contributing to enhanced invasiveness (Richardson and Rejmánek 2004). Introduced species are also grown in large-scale plantations using cultivation techniques that enhance survival rates, which lowers the probability of local extinctions and creates a massive propagule pressure, increasing the probability of them escaping from cultivation (Mack 2005; Křivánek et al. 2006; Pyšek et al. 2014). For example, in the Czech Republic, 25% of tree species introduced for forestry have become invasive (Pyšek 2016). Most invasive trees in Europe are light-demanding and have better

invasion success in disturbed habitats (Richardson and Rejmánek 2004; Meloni et al. 2016). However, shade-tolerant species also exhibit invasive behavior once introduced to mature forests with low disturbance. For instance, *Prunus serotina* invaded the undergrowth of forests in western Europe (Hernandez et al. 2016).

Conifers in particular have been introduced to many areas and were widely planted for timber production, providing substantial opportunity for invasion (Richardson and Rejmánek 2004; Broncano et al. 2005). Globally, 36 species of conifers are already considered invasive (Richardson and Rejmánek 2004) with alien conifers used in commercial forestry having a significantly higher probability of escaping cultivation compared to species not used for timber production (Essl et al. 2010). Conifers are still not often perceived as problematic in Europe because their invasions have been primarily documented in the southern hemisphere so far. Yet, studies indicate that alien conifers are showing invasive behaviors in Europe, too (Carrillo-Gavilán and Vilà 2010; Essl et al. 2010). If the planting of alien species in European forests continues, which is likely to happen with the dieback of several native species, it is necessary to distinguish high risk species from those that are unlikely to become invasive (Dodet and Collet 2012; Heger 2016).

Forest trials and arboreta offer the opportunity to monitor the regeneration dynamic of exotic species, acting as sentinel sites of which careful observations could facilitate the detection of new invasions (Carrillo-Gavilán and Vilà 2010). These areas are also likely to act as sources of propagules and sites of entry for new invasions (Richardson and Rejmánek 2004; Brundu and Richardson 2016). During the 19th century, the Belgian Forest Department started to diversify forests plantations with exotic species. A network of 23 forest arboreta was set up between 1890 and 1914 throughout the country to monitor the growth and wood production potential of both native and alien species, especially ones from Japan and the west coast of North America (Nyssen et al. 2016). The arboreta were implemented in various ecological regions to cover the diversity of climates and soil types of the country. Every arboretum differed in its setup and list of species. Unfortunately, the geographical origin of the seeds remains unknown. Recently, a new interest in these arboreta emerged and new inventories were performed in 2016 to study the production potential of exotic species in the light of climate change (Lhoir and Scholzen 2017). In several of these arboreta, no management actions of the understory were implemented over the last 15 years except for clearing the pathways. The natural regeneration is therefore mostly untouched.

In this study, we aimed to identify alien conifer species presenting invasive potential. To do so, we systematically quantified the natural regeneration of alien species in and around eight selected arboreta. Richardson et al. (2000) defined invasive plant species as species producing reproductive offspring in very large numbers and at considerable distances from parent plants. By combining information on tree density, realized dispersal, and the size structure of the natural regeneration of alien conifers, we assessed their invasive potential. Specifically, we evaluated i) the density of natural regeneration and the realized dispersal distances from nearest parent trees; ii) whether a diverse size structure exists in the natural regeneration of species that regenerated;

and iii) the influence of tree-stand type and environmental conditions on the regeneration density of species of highest concern. The correlation between the regeneration density and traits linked to invasiveness in previous studies was also assessed.

Material and methods

Study area

The study area covered the Walloon Region in Southern Belgium (49.5966°N to 50.5705°N latitude, 4.5469°E to 5.8852°E longitude). Eight arboreta, further referred to as "sites", were selected (Fig. 1) based on three criteria: i) at least 15 planted alien conifer species, ii) no management actions in the understory that would have influenced the natural regeneration for the last 15 years, and iii) information being available on plantation dates.

In this study species were considered alien when they did not naturally occur in continental Europe. Sixty-nine percent of the total planted area within the arboreta was occupied by alien conifers. Only 8% percent was planted with European conifers (mainly *Picea abies* and *Abies alba*). The remaining area was planted with native and alien broadleaves. All the arboreta consist of forest ecosystems, even though a few small clearings with solitary individuals could be found. Thus, the planted area varied greatly across species, from 6 m^2 to 9.1 ha.

Sampling procedures

Field sampling was conducted from April to July 2018. Sampling was systematic and covered the entire arboreta and a 100-m buffer, representing a total of 129.5 ha. For each arboretum, a 30×30 m grid was applied and a plot was installed at each intersection, generating 1565 plots. Sampling plots consisted of circles of 2-m radius. Plots situated on roads, ponds, private land, and recent forest plantings were excluded along with sites with insecure access, such as rocky scree. In total, 1109 plots were sampled in forested areas (from 71 to 244 plots per arboretum). In each plot, all individuals of alien conifer species (from young seedlings to adult trees) were recorded and their height measured from the ground to the tip of the main stem. They were then assigned to the following size classes: class 0 for seedlings between 0 and 0.3 m high, class 1 for saplings between 0.3 m and 1.3 m high (height of measurable diameter at breast height, DBH), class 3 for trees higher than 1.3 m but with DBH smaller than 5 cm, class 4 for trees with DBH between 5 and 9.9 cm, and so on for every 5 cm increment in DBH.

Identifying seedlings was sometimes challenging and 1878 fir seedlings (including 850 in only one plot) were excluded from further analyses, as it was not possible to determine species with certainty due to their stage of development (probably *A. grandis* or *A. alba*). The regeneration data for *Abies* species was therefore underestimated.

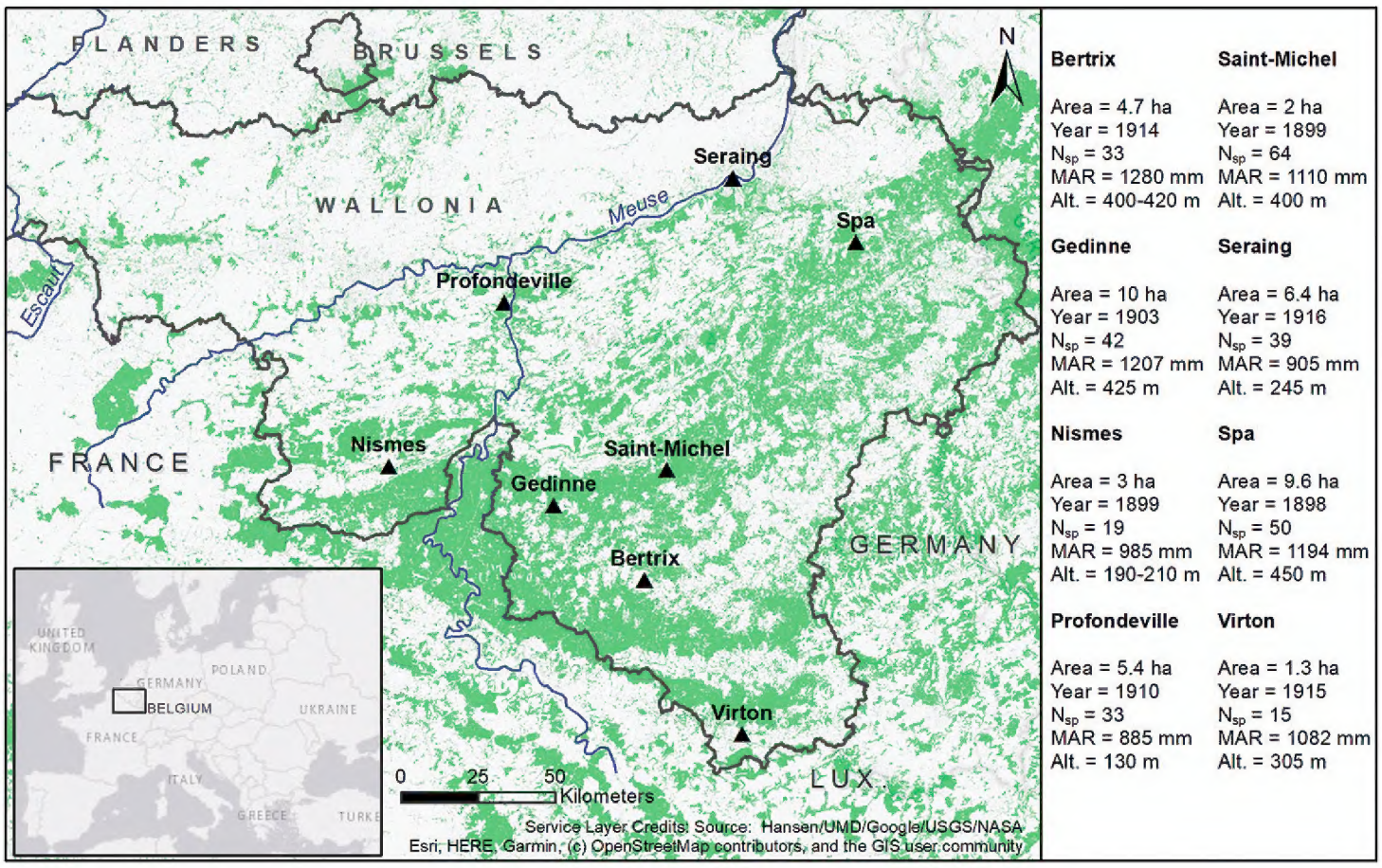

Figure 1. Location and description of the arboreta used in this study (triangle symbols) on a background map of tree cover in 2000 (Hansen et al. 2013). For each arboretum, the following characteristics were obtained: Year = year of first plantings, N_{sp} = number of alien conifer species planted in the arboretum, MAR = Mean Annual Rainfall between 1981 and 2010 obtained from the Royal Meteorological Institute of Belgium (RMI, n.d.), and Alt. = Altitude (m).

We measured environmental variables that influence the settlement of species (Dyderski and Jagodziński 2018). The thickness of litter (mm) was measured with a ruler at four different places in the plot and the mean was calculated (ranging from 0 to 100 mm, median = 20 mm, mean = 24.14 mm). The pH was measured with a pH-kit on the field in the center of the plot with a precision of 0.5 units (range: 4 to 6.5, median = 4.0, mean = 4.3). Canopy openness was assessed with a spherical convex densiometer in four cardinal directions (Forestry Supplier spherical crown densiometer, Convex – Model A), and ranged from 0.2 to 90.2 % (median = 7.2 %, mean = 11.1 %). Soil drainage was attributed from the plot geographical coordinates based on the Digital Soil Map of Wallonia (Bah et al. 2007; Service Public de Wallonie 2019). Soils ranged from being excessively well-drained (1) to poorly drained (5). Soil drainage classes are defined according to soil morphological attributes, more precisely the depth of appearance of gleyic color pattern reflecting the presence of stagnant water (Bah et al. 2007). Most soils were excessively well-drained (median = 1, mean = 1.89). Out of the 1109 prospected plots, the tree-stand type was defined: 545 plots were under coniferous stands, 557 plots were under broadleaved species (mainly *Fagus sylvatica* in the buffer zones), and seven plots were in open areas (clear-cuts).

Statistical procedures

A generalized linear mixed effect model (GLMM) with Poisson family was used to determine whether there was a significant influence of several variables on the regeneration ability of alien species regenerating in at least two sites. The lme4 package was used (Bates et al. 2015). The fixed variables were the species, the area of plantation, the time since plantation, the distance to the nearest parent trees, and the tree-stand type (broadleaves, open areas, European conifers or exotic conifers). The exact number of planted trees per species was unknown. We therefore used the area of plantation as a proxy for the propagule pressure, as the density of plantation was similar for the coniferous species. The site and the plot nested within the site were included as random effects. Zero-inflation was tested and not detected. A significant p value threshold was set at 0.05. An ANOVA with the "car" package was performed on the regression result (Fox and Weisberg 2019).

The two first key determinants of invasiveness that we analyzed were the density of regeneration and dispersal distances from the closest parent trees. Regeneration Density (RD) was calculated for every species as the mean number of individuals per ha. For the capacity of regeneration of different species to be comparable, we calculated the Weighted Regeneration Density (WRD) which represented the density of regenerating individuals per ha for 1 ha planted of the same species. The WRD was calculated by dividing the regeneration density (RD) in each plot by the planted area of species in the corresponding arboretum. Because WRD is the density of individuals (indiv.ha^{-1}) divided by an area (ha), the unit is indiv.ha^{-1}.ha$_{planted}^{-1}$. For each species in each plot, the realized dispersal distance (DD) was measured as the distance to the nearest planted parent trees with ArcMap v. 10.5.1 (ESRI 2019). For species with at least 10 individuals found in the regeneration, boxplots and density plots of the distribution of dispersal distances were constructed. As long-distance dispersal events are of major importance in the invasion process, the 95th percentile of distribution of distances was represented to characterize the tail (Higgins and Richardson 1999; Monty et al. 2013). A "summary plot" (Fig. 2B) combining the WRD and 95th percentile of dispersal distances was built to characterize the behaviors of species visually regarding these two aspects of invasiveness. The plots and analyses were performed using R software (R Core Team 2020).

Richardson et al. (2000) delineated a threshold of 100 m in 50 years as a rule of thumb for the dispersal of an alien plant defined as invasive (Richardson and Rejmánek 2004; Nygaard and Øyen 2017). To compare dispersal observed in the arboreta with the threshold provided in this definition, dispersal distances over 50 years (DD50) were also calculated. Dispersal distances (DD) for every individual were divided by the time since planting minus the age of maturity of the species, and were then multiplied by 50 (Eq. 1). Data on the age of maturity were compiled from Kattge et al. (2011), Petit et al. (2017), and Forestry Commission Scotland (2015).

$$DD50 = \frac{DD \times 50}{time\ since\ planting - age\ of\ maturity} \qquad \text{(Eq. 1)}$$

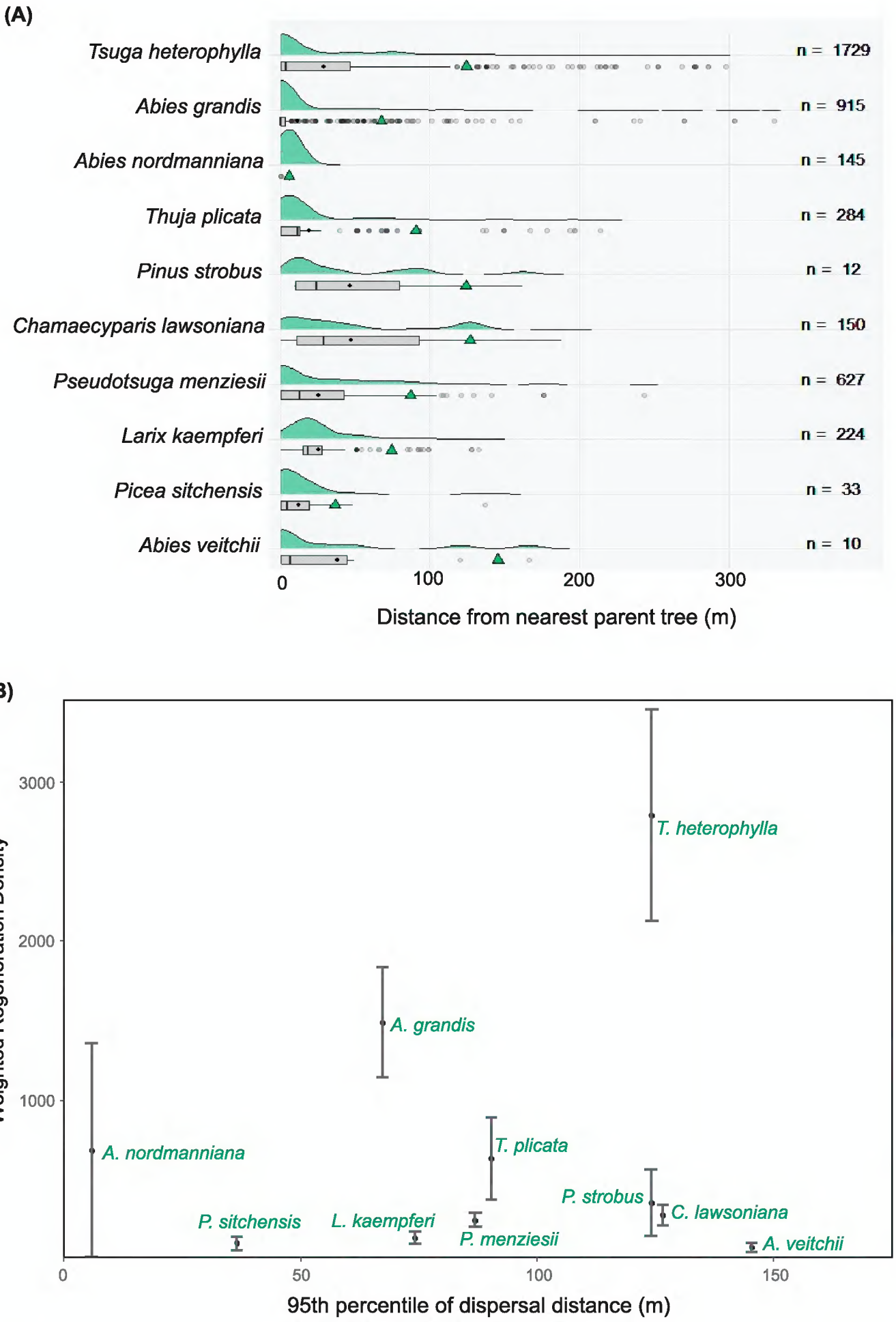

Figure 2. Regeneration density and dispersal of alien conifers **A** boxplots and density plots of dispersal distances for species of which at least 10 individuals were recorded. Species are ordered in descending order using WRD. The total number of individuals per species (n) is indicated on the right. The mean (point) and median (vertical bar) are indicated. The 95th percentile was also represented with a green triangle **B** comparison of species based on mean WRD ± standard error (indiv.ha^{-1}.ha$_{planted}^{-1}$) and 95th percentile of dispersal distances (m).

Because an invasive species must be capable of producing mature offspring, the size structure of natural regeneration was also observed. A table on size structure was constructed for the 10 species with at least 10 measured individuals to examine the viability of the natural regeneration.

We investigated whether the most invasive species occupy a wide range of environmental conditions. We selected species presenting a combination of important regeneration density (WRD > 100 indiv.ha^{-1}.ha$_{planted}^{-1}$), high dispersal distance (Perc. 95 > 50 m), and a developed size structure with older individuals (DBH > 10 cm). To detect environmental gradients through the measured plots, we performed a principal component analysis (PCA) on the environmental matrix containing all plots and the four quantitative environmental variables using the ade4 package (Dray and Dufour 2007). The plots in which the selected species were regenerating were projected in the environmental space made by the first two Principal Components. Density lines for each species on the two axes of the PCA were drawn, allowing us to delineate the environmental space occupied by each species. This method is widely used to estimate niche overlap of species (Broennimann et al. 2012).

Finally, data was gathered for two traits associated with invasiveness, namely the seed mass and the maximal height of the species, both linked to the capacity to disperse at long distances (Richardson and Rejmánek 2004; Kutlvašr et al. 2019). Data was compiled from Greene and Johnson (1993), Kattge et al. (2011) and Johnson and More (2014). As a Shapiro-Wilk test rejected the normality of our variables, we performed a non-parametric Kendall correlation test on these two variables related to the Weighted Regeneration Density of all species planted in at least half of the arboreta.

Results

In total, 1109 plots were surveyed and 4148 individuals recorded, from small seedlings to mature trees over 60 cm of DBH. Due to the size of the sampling plots, we never found more than one non-planted tree with a DBH > 20 cm in one plot. These individuals belonged to 31 alien conifer species planted between 1898 and 1916 in eight arboreta across the Walloon Region (Table 1). For 15 of the planted species, no regeneration was detected, while six species had less than 10 individuals recorded across all sites. In contrast, some species presented abundant regeneration. The most frequent seedlings encountered were *Tsuga heterophylla* and *Abies grandis*. The planted area, time since planting and distance to the nearest parent trees significantly affected the density of regeneration (Table 2). We further used the Weighted Regeneration Density (WRD) for between-species comparison.

Tsuga heterophylla was the most represented alien conifer in natural regeneration with a WRD of 2794.0 indiv.ha^{-1}.ha$_{planted}^{-1}$. This species was followed by *Abies grandis* (WRD = 1493.8 indiv.ha^{-1}.ha$_{planted}^{-1}$), *Abies nordmanniana* (688.3 indiv.ha^{-1}.ha$_{planted}^{-1}$) and *Thuja plicata* (637.8 indiv.ha^{-1}.ha$_{planted}^{-1}$).

Table 1. List of species planted in at least four of the eight selected arboreta. **N sites planted** = number of arboreta where species were planted. **Native distribution** of species is also given. **Planted area** = total planted area of species in all sites. **N sites found** and **N plots** are the number of sites (arboreta) and plots (1109 plots in total) where the natural regeneration of species occurred. **N indiv.** = number of trees recorded in natural regeneration. For each plot, the regeneration density (**RD)** in indiv.ha^{-1} and weighted density of regeneration (**WRD)** in indiv.ha^{-1}·ha$_{planted}^{-1}$ were calculated, and the mean is given in the table. The median, maximum, and 95th percentiles of dispersal distance distributions are given (**Median DD**, **Max DD** and **Perc. 95 DD**). The maximum dispersal distance over 50 years (**Max DR50**) and the 95th percentile (**Perc. 95 DR50**) were calculated.

Species	Native distribution	Planted area	N sites planted	N sites found	N plots	N indiv.	Mean RD	Mean WRD	Median DD	Perc. 95 DD	Max DD	Perc. 95 DD 50	Max DD50
Tsuga heterophylla	North America	2,1	8	6	136	1729	1240,7	2794,0	3,8	124,3	298,0	84,3	201,3
Abies grandis	North America	1,803	8	6	103	915	656,6	1493,8	0,0	67,4	330,1	39,5	177,5
Abies nordmanniana	Caucasus	0,581	6	2	4	145	126,2	688,3	5,8	5,8	5,8	4,03	4,0
Thuja plicata	North America	1,567	8	4	39	284	203,8	637,8	11,2	90,3	213,8	54,9	127,2
Pinus strobus	North America	0,325	6	2	9	12	10,7	357,8	23,9	124,2	162,2	73	95,4
Chamaecyparis lawsoniana	North America	2,088	8	5	46	150	107,6	279,4	28,7	126,7	187,7	77,3	120,3
Pseudotsuga menziesii	North America	9,011	8	6	177	627	449,9	248,8	12,8	87,0	243,3	40,4	95,0
Chamaecyparis obtusa	Japan	0,08	5	1	2	4	4,7	243,8	7,0	7,0	7,0	4,5	4,5
Larix kaempferi	Japan	3,247	8	3	39	224	160,7	136,6	18,1	74,3	132,3	49,5	88,2
Abies cilicica	Middle-East	0,09	4	1	1	3	4,2	117,0	2,9	2,9	2,9	2,3	2,3
Chamaecyparis pisifera	Japan	0,236	6	1	1	6	4,6	116,3	0,8	0,8	0,8	0,5	0,5
Picea sitchensis	North America	0,789	4	2	9	33	37,1	104,2	4,2	36,5	136,7	33,8	126,5
Abies homolepis	Japan	0,336	6	2	2	4	3,3	84,8	0,0	15,9	18,7	15,9	25,2
Abies veitchii	Japan	0,578	5	3	7	10	9,3	76,6	6,6	145,4	166,0	125	133,9
Abies procera	North America	0,352	5	1	1	1	0,9	20,7	0,0	0,0	0,0	0	0,0
Picea orientalis	Caucasus	0,294	7	1	1	1	0,8	8,5	5,7	5,7	5,7	4,4	4,4
Abies concolor	North America	0,294	5	0	0	0	0	0	–	–	–	–	–
Abies numidica	North Africa	0,122	4	0	0	0	0	0	–	–	–	–	–
Cedrus libani	Middle-East	0,049	4	0	0	0	0	0	–	–	–	–	–
Cryptomeria japonica	Japan	0,265	8	0	0	0	0	0	–	–	–	–	–
Metasequoia glyptostroboides	Asia	0,281	6	0	0	0	0	0	–	–	–	–	–
Picea engelmannii	North America	0,236	4	0	0	0	0	0	–	–	–	–	–
Picea glauca	North America	0,14	4	0	0	0	0	0	–	–	–	–	–
Picea jezoensis	Asia	0,107	5	0	0	0	0	0	–	–	–	–	–
Picea koyamae	Japan	0,234	6	0	0	0	0	0	–	–	–	–	–
Picea rubens	North America	0,143	4	0	0	0	0	0	–	–	–	–	–
Picea torano	Japan	0,115	4	0	0	0	0	0	–	–	–	–	–
Pinus ponderosa	North America	0,141	4	0	0	0	0	0	–	–	–	–	–
Sequoiadendron giganteum	North America	0,244	7	0	0	0	0	0	–	–	–	–	–
Tsuga canadensis	North America	0,238	5	0	0	0	0	0	–	–	–	–	–
Xanthocyparis nootkatensis	North America	0,045	4	0	0	0	0	0	–	–	–	–	–

Table 2. Results of the generalized linear mixed effect model on the count of regeneration. Estimates, standard errors, Z values and p values are given for fixed effects.

Variable		Estimate	Std. Error	Z value	p value
Species	*Abies grandis*	(base)			
	Abies homolepis	-3.17E+00	4.63E-01	-6.85	< 0.001
	Abies nordmanniana	-5.55E-01	1.17E-01	-4.744	< 0.001
	Abies veitchii	-2.28E+00	3.20E-01	-7.121	< 0.001
	Chamaecyparis lawsoniana	-9.86E-01	1.09E-01	-9.078	< 0.001
	Larix kaempferi	-6.29E-01	1.12E-01	-5.61	< 0.001
	Picea sitchensis	-9.07E-01	1.85E-01	-4.9	< 0.001
	Pinus strobus	-2.79E+00	2.82E-01	-9.902	< 0.001
	Pseudotsuga menziesii	-2.40E+00	1.10E-01	-21.872	< 0.001
	Thuja plicata	-2.74E-01	9.48E-02	-2.894	0.00381
	Tsuga heterophylla	1.84E+00	8.61E-02	21.336	< 0.001
Canopy type	Broadleaves	(base)			
	European conifers	1.28E+00	8.64E-02	14.862	< 0.001
	Exotic conifers	1.46E+00	7.58E-02	19.259	< 0.001
	Open areas	3.61E+00	1.73E-01	20.869	< 0.001
Time since plantation		5.24E-02	3.15E-03	16.638	< 0.001
Surface planted		5.56E-05	3.24E-06	17.179	< 0.001
Distance from plantation		-2.16E-02	5.69E-04	-37.956	< 0.001

Table 3. Size class distribution of percentages for species with more than 10 recorded individuals. The two first classes are composed of individuals smaller than 1.3 m, for which DBH could not be calculated. The other classes were based on DBH intervals (cm). Classes were aggregated to improve readability.

		Height (m)		DBH (cm) | H > 1.3 m					
Species	*N*	0–0.3	0–1.3	< 5	5–10	10–20	20–30	30–50	> 60
A. grandis	939	53.2	34.6	11.4	0.5	0.2	0	0	0
A. nordmanniana	145	98.6	1.4	0	0	0	0	0	0
A. veitchii	10	30	40	30	0	0	0	0	0
C. lawsoniana	163	39.3	30.7	20.2	8.0	1.2	0	0	0.6
L. kaempferi	227	52.4	31.7	14.5	0	0.4	0.9	0	0
P. menziesii	623	64.5	23.6	7.7	1.9	1.3	0.6	0	0.3
P. sitchensis	15	100	0	0	0	0	0	0	0
P. strobus	9	100	0	0	0	0	0	0	0
T. heterophylla	1732	80.1	9.2	9.5	0.8	0.2	0.1	0.1	0
T. plicata	287	49.1	38.3	10.8	0.7	0.3	0	0.7	0

Ten species had at least 10 seedlings recorded in the natural regeneration. They tended to be found close to parent trees (Fig. 2A). However, the seedlings of nine species were sometimes detected at >100 m distance from possible parent trees. Four species had a 95th percentile for dispersal distance distribution exceeding 100 m. Only *Abies nordmanniana* displayed very low dispersal distances, with all recorded individuals occurring within 6 m of planted parent trees. The maximal DD exceeded 200 m for the seedlings of *Tsuga heterophylla*, *Pseudotsuga menziesii*, and *Thuja plicata*, and even 300 m for *Abies grandis*.

For the same 10 species with 10 recorded individuals, size structure was used to investigate the survival of the regeneration. Ninety-three percent of recorded trees in natural regeneration were <1.3 m high. All individuals of *P. sitchensis* and *P. strobus* were seedlings <0.3 m high (Table 3). However, older trees with a DBH >20 cm were detected for *C. lawsoniana*, *P. menziesii*, *T. plicata*, *L. kaempferi*, and *T. heterophylla*.

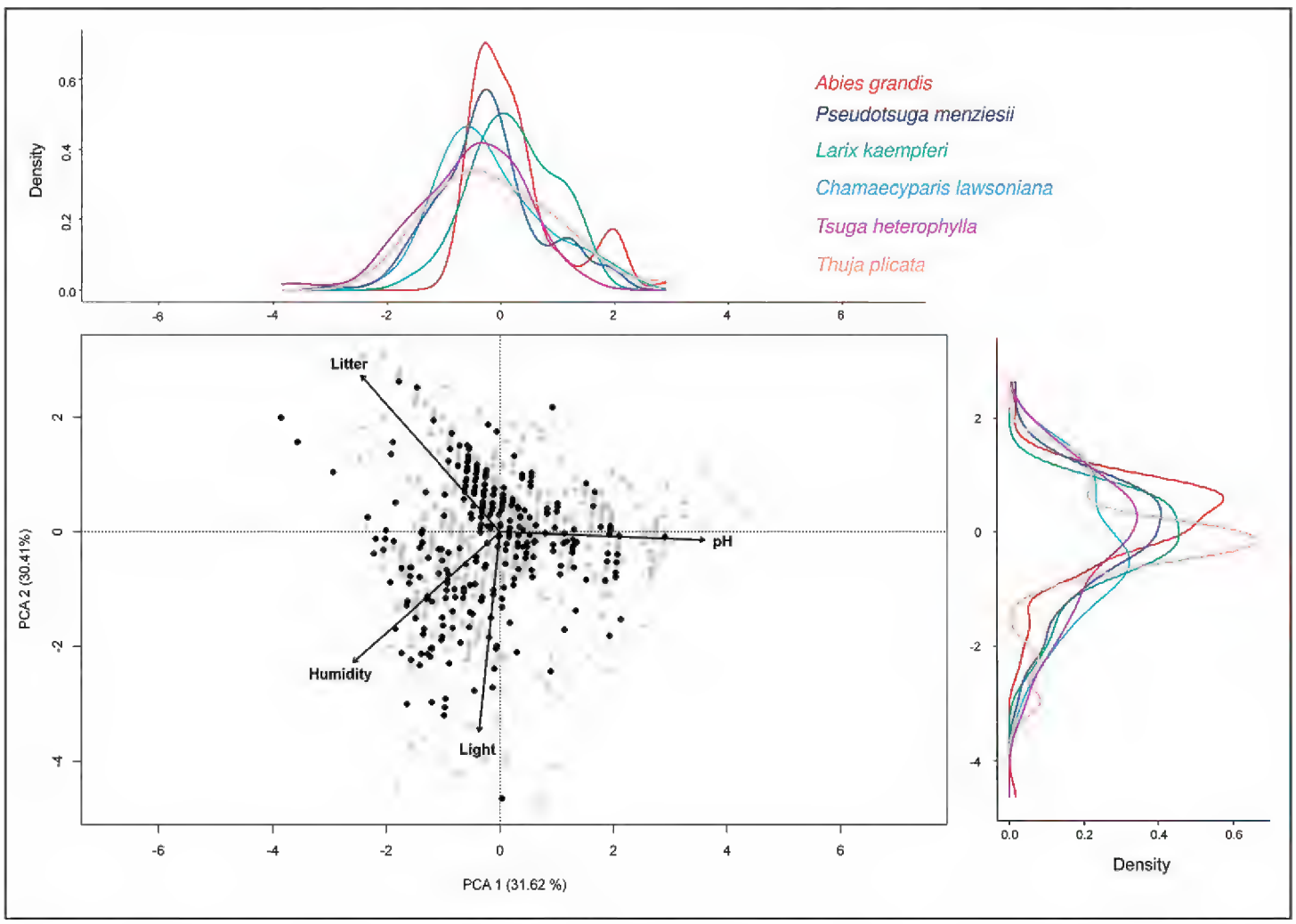

Figure 3. Distribution of alien conifers in the environmental space. Regeneration of six conifers in the environmental space made by the two first axes of the PCA. The circle of correlation of four environmental variables was projected on the graph: pH, litter thickness, canopy openness (referred to as "Light"), and soil drainage class (referred to as "Humidity"). The percentage of explained variance for each Principal Component is indicated. Dots represent all plots of the eight arboreta. Black dots are those in which at least one of the six species is regenerating. Density lines are drawn for each species along the two axes of the PCA.

Though conifers and broadleaved stands were almost equally represented in the plot data, alien conifers mainly regenerated under coniferous stands. Specifically, 69% of individuals were found under exotic conifers, 18 % under European conifers, 7% in clear-cut areas, and only 6% under broadleaved species. Open areas and exotic coniferous stands significantly increased the regeneration count of alien conifers (Table 2).

From the principal component analysis (Fig. 3), two environmental gradients were identified and were regulated by soil pH (first Principal Component, PC1) and canopy openness (PC2). Wet soil tended to be more acidic. Litter was thicker on acidic plots with low light availability. Along these gradients, we projected the presence of six species showing a combination of important WRD (>100 indiv.ha^{-1}.ha$_{planted}^{-1}$), high dispersal distance (perc. 95 > 50 m), and developed size structure (individuals >10 cm DBH): *Tsuga heterophylla*, *Abies grandis*, *Thuja plicata*, *Chamaecyparis lawsoniana*, *Larix kaempferi*, and *Pseudotsuga menziesii*. We found that these species occupied a wide range of environmental conditions of the arboreta, including areas with low canopy openness. Ecological niches and optimums of presence were rather similar for the six species. *Abies grandis* also occurred on dry and basic soils.

Kendall's correlation highlighted a significant positive relationship between the height of species and their WRD (tau=0.459, z=3.096, p value = 0.002). On the other hand, the correlation was not significant for the seed mass (tau = -0.064, z=-0.411, p value = 0.681).

Discussion

This study demonstrated that alien conifers naturally regenerated in each arboretum that was visited, sometimes in dense patches of seedlings. Of the 31 alien species considered, 16 were detected regenerating. Eleven species (35%) had a Weighted Regeneration Density of more than 100 indiv.ha^{-1}.ha$_{planted}^{-1}$. The planted area and the time since plantation both had a positive significant effect on the count of regeneration, confirming the important influence of the propagule pressure on the regeneration of alien species (Lockwood et al. 2009; Pyšek et al. 2009).

Most species primarily regenerated close to parent trees. Long dispersal events of over 100 m were detected for nine species. For the prolific species *Tsuga heterophylla*, five percent of regeneration occurred past 124 m, and some even reached 300 m one century after planting. Thus, long-distance dispersal events are frequent for this species. The 95th percentile of dispersal distance also exceeded 100 m for *P. strobus*, *C. lawsoniana*, and *Abies veitchii*. However, the prospected area was limited, with even longer distances from the closest parent trees being possible. Our estimates of long-dispersal distances can therefore be considered conservative. Given the importance of long-distance dispersal events in the invasion process, more exhaustive inventories of the dispersal potential of these species along transects are required until no individual is found for a given distance lapse (Higgins and Richardson 1999).

The weighted regeneration density and the dispersal distance are useful tools for monitoring the invasive behavior of alien conifers. However, as invasive species must maintain viable populations, the age structure of natural regeneration must be incorporated (Wilson et al. 2014). For *A. nordmanniana*, the high number of individuals was attributed to a single large germination event resulting in hundreds of seedlings of less than one-year-old being detected in one plot; 142 out of the 145 individuals recorded were young seedlings beneath a parent tree, indicating that most regeneration is not viable. *Pinus strobus* and *P. sitchensis* seedlings were recorded at further distances, but only seedlings smaller than 0.3 m were found. In comparison, *T. heterophylla*, *P. menziesii*, *A. grandis*, *C. lawsoniana*, *L. kaempferi*, and *T. plicata* also tended to exhibit large germination events beneath parent trees but older trees were also recorded (see Table 3), including mature ones. Thus, these species likely have the capacity to create new satellite populations.

The question of whether some species cross the benchmark of 100 m dispersal distance over 50 years was evaluated in this study. Richardson et al.(2000) stated that, for a species to be invasive, there must be "clear evidence that it regenerated naturally and recruited seedlings more than 100 m from parent plants". This distance is associated

with a time-lapse of 50 years since introduction, and reproductive offspring must be found beyond 100 m. These events involve the tail of the dispersal curve, as only a small number of long-distance dispersal events producing reproductive offspring is necessary to create a new population at a far distance. Individuals of *A. grandis*, *T. heterophylla*, *T. plicata*, *C. lawsoniana*, *P. sitchensis*, and *A. veitchii* occurred over a DD50 of 100 m. If no mature individuals were measured, individuals taller than 1.3 m were recorded for *A. grandis* and *T. heterophylla* over the specified distance. It means they survived the most vulnerable seedling stage, and could potentially grow to sexual maturity.

Six species exhibited high invasive potential based on the three studied factors: *T. heterophylla*, *A. grandis*, *T. plicata*, *C. lawsoniana*, *L. kaempferi*, and *P. menziesii*. They were selected for the environmental analysis. Once projected on the PCA, these six species occupied a large proportion of the environmental space encountered at the surveyed sites, and displayed generalist behavior across common environmental conditions. Of note, *T. heterophylla* preferentially regenerated on acidic soils, supporting existing knowledge on the ecological preferences of this species (Rooney et al. 2000). In comparison, *A. grandis* tolerated drier soils, which might be beneficial under climate change as water stress is likely to become more frequent in the near future (Campioli et al. 2009). An important regeneration was recorded in open areas resulting from clear cuts. Interestingly, these six species also exhibited shade tolerance during regeneration with many individuals occurring in plots with low canopy openness, allowing them to spread in closed forest ecosystems. Martin and Marks (2006) demonstrated that invasions of undisturbed forests by shade-tolerant alien species frequently occur but require a longer time span than invasions in disturbed habitats, resulting in their invasiveness often being underestimated. The combination of a generalist behavior across soil types and shade-tolerance could allow these alien conifers to invade mature, undisturbed forests. This phenomenon is likely to be facilitated by areas planted with conifers. Consequently, because of the capacity of conifers to transform habitat, increasing the proportion of coniferous stands in wood production forests might accelerate the invasion rate of alien conifers (Jagodziński et al. 2015). In 2011, 48 % of the southern Belgium forest was planted with conifers (Lecomte 2017). *Pseudotsuga menziesii* represented 6 % of the surface inventoried by the Belgian permanent forest inventory in 2011, far more than the other species highlighted in our study, and its proportion has increased by 52% since 2001. *Larix* sp., *A. grandis*, *T. plicata*, *T. heterophylla* and *C. lawsoniana* together represent a marginal section inventoried surface in 2011, and it is difficult to know the real extent of these species in public and private forests (Bauwens 2020). However, trials with alien species are becoming more frequent (Richardson et al. 2014), and exotic conifers are more and more considered as replacement species to compensate for the die-back of native productive species. For example, *C. lawsoniana* and *T. plicata* are selected for the REINFFORCE arboreta network, aiming to collect data on the growth of alien species in view of the diversification of European Atlantic temperate forests in light of climate change (Orazio et al. 2013).

Our sampling covered a large diversity of environmental conditions met in southern Belgium forests, from calcareous to acidic soils, from forests dominated by native

broadleaves to spruce plantations. These species can potentially invade a large proportion of forest lands, especially productive lands planted with conifers and managed with clear-cut regimes. However, this study did not cover the full diversity of temperate forests in Western Europe, with wider gradients potentially generating greater differences in the environmental space occupied by each species.

These six highlighted species also exhibit invasive behavior in other European countries (Rejmánek and Richardson 2003; Richardson and Rejmánek 2004; Broncano et al. 2005; Orellana and Raffaele 2010; Forestry Commission Scotland 2015). In western Norway, *T. heterophylla* is considered to be a very invasive conifer due to its high potential for spreading into neighboring stands and clear cuts (Oyen 2001). Plantations of *T. heterophylla* generate intense shade with few plants being able to live beneath them (Harmer et al. 2011). Galoux (1951) demonstrated the high regeneration capacity of *T. heterophylla* in Belgian arboreta, mentioning dense regeneration patches that occur beneath seed-bearers and in the neighboring plantations. The same author also stressed the abundant seed production and regeneration potential of *C. lawsoniana*, *P. menziesii*, and *A. grandis*. As the report was written in the middle of the 20th century, we know that the natural regeneration of these species has been ongoing for at least 70 years in the arboreta.

A small seed mass and an important maximal height have been linked to a better invasion success of plants in previous studies (Richardson and Rejmánek 2004, van Kleunen et al. 2010; Kutlvašr et al. 2019). Both traits are linked with the capacity of species to spread at long distances. We did find a positive correlation between the maximal height and the Weighted Regeneration Density, but not with the seed mass. Dawson et al. (2011) surveyed exotic plants escaping from a tropical botanical garden. They concluded that propagule pressure was of greater significance than the functional traits in the establishment of alien plants in natural habitats. In a study conducted in North America, Pyšek et al. (2015) concluded that the importance of biological traits is highly dependent on the invasion stage, and often over-estimated. Further investigation on the role of functional traits on the invasiveness should be led in the local conditions of the Belgian arboreta, including the relative growth rate and specific leaf area, to test whether similar conclusions can be drawn.

The species exhibiting an important invasive potential in our study could be part of the invasion debt *sensu* Rouget et al. (2016) in Belgian forests. The important lag phase might be misleading concerning the potential impact of alien conifers, especially *T. heterophylla*. Twenty percent of the studied species exhibited invasive tendencies and they will certainly continue to expand in the future, especially if planting effort increases. In comparison, we did not detect any regeneration for half of the studied species. If foresters want to diversify forest plantations, they should avoid introducing species with high invasiveness and prefer native species or low-risk alien species (Brundu et al. 2020).

We identified species that were likely to become invasive based on small forest trials. The effect of mass plantings was not addressed. However, we demonstrated that the size of planted areas positively impacts regeneration density. Previous studies showed that propagule pressure has the potential to overwhelm ecological resistance

of ecosystems to invasions (Von Holle and Simberloff 2005). Even species considered to be dispersal-limited but with strong potential for wood production might cross a propagule pressure threshold and become invasive in the future due to high planting intensity (Richardson et al. 2004; Jagodziński et al. 2018).

Ennos et al. (2018) demonstrated that using non-native species for wood production and the diversification of forests presents great ecological and economic risks, potentially to the detriment of native tree species and associated biodiversity. Based on experience in countries with longer histories of using alien conifers, along with objectives to prevent further ecological damage, risk analyses of introduced alien conifers must be performed by monitoring old forest trials and arboreta (Richardson and Rejmánek 2004).

Conclusion

Given the observed natural regeneration and dispersal of alien conifers in the old forest arboreta of southern Belgium, we recommend exercising caution when planting them in western temperate Europe. Half of the studied species regenerated, with almost 20% of these exhibiting an invasive behavior. Species showing the highest risk of being invasive were *T. heterophylla* and *A. grandis*, and to a lesser extent *C. lawsoniana*, *T. plicata*, *L. kaempferi*, and *P. menziesii*. Species with more limited dispersal capacities or a lesser proportion of mature trees, such as *A. nordmanniana*, *P. strobus*, *P. sitchensis*, and *A. veitchii*, could become of concern if planted at large scales. The results show that forest arboreta act as entry points for invasive species, especially now that more forestry trials are being set up to compensate for the die-off of native productive species. Thorough monitoring of alien conifers introduced for wood production is therefore needed to take early action for control and avoidance of larger introductions.

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